

THE DETERMINANTS OF THE STEP FREQUENCY IN RUNNING, TROTTING AND HOPPING IN MAN AND OTHER VERTEBRATES

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SUMMARY

1. During each step of running, trotting or hopping part of the gravitational and kinetic energy of the body is absorbed and successively restored by the muscles as in an elastic rebound. In this study we analysed the vertical motion of the centre of gravity of the body during this rebound and defined the relationship between the apparent natural frequency of the bouncing system and the step frequency at the different speeds.

2. The step period and the vertical oscillation of the centre of gravity during the step were divided into two parts: a part taking place when the vertical force exerted on the ground is greater than body weight (lower part of the oscillation) and a part taking place when this force is smaller than body weight (upper part of the oscillation). This analysis was made on running humans and birds; trotting dogs, monkeys and rams; and hopping kangaroos and springhares.

3. During trotting and low-speed running the rebound is symmetric, i.e. the duration and the amplitude of the lower part of the vertical oscillation of the centre of gravity are about equal to those of the upper part. In this case, the step frequency equals the frequency of the bouncing system.

4. At high speeds of running and in hopping the rebound is asymmetric, i.e. the duration and the amplitude of the upper part of the oscillation are greater than those of the lower part, and the step frequency is lower than the frequency of the system.

5. The asymmetry is due to a relative increase in the vertical push. At a given speed, the asymmetric bounce requires a greater power to maintain the motion of the centre of gravity of the body, \dot{W}_{ext} , than the symmetric bounce. A reduction of the push would decrease \dot{W}_{ext} but the resulting greater step frequency would increase the power required to accelerate the limbs relative to the centre of gravity, \dot{W}_{int} . It is concluded that the asymmetric rebound is adopted in order to minimize the total power, $\dot{W}_{\text{ext}} + \dot{W}_{\text{int}}$.

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INTRODUCTION

Legged vertebrate locomotion apparently involves only two basic mechanisms: the rigid mechanism of walking (similar to an 'inverted pendulum') and the compliant mechanism of running, trotting and hopping (similar to a 'bouncing ball'; Cavagna, Heglund & Taylor, 1977). In walking, the gravitational potential energy and kinetic energy changes of the centre of gravity of the body are almost completely out of phase (Cavagna, Saibene & Margaria, 1963) whereas in running they are in phase (Cavagna, Saibene & Margaria, 1964). The in-phase oscillation of the kinetic and potential energy of the centre of gravity in running is suggestive of an elastic rebound of the body as the energy is alternately absorbed and restored by the muscles. Although the bouncing mechanism of running is now widely accepted, it is poorly substantiated by experimental evidence.

The step period is usually divided into ground contact time, during which storage and release of mechanical energy is thought to occur, and a ballistic aerial phase. The ground contact time is believed to be shorter the stiffer the elastic bouncing system (Cavagna, Thys & Zamboni, 1976) and to be equal, as a first approximation, to one-half the natural period of the system (McMahon, 1985). As will be shown below, this approach is misleading.

In each step of running, the vertical motion of the centre of mass of the body is reversed due to gravity and the impact against the ground. It is therefore reasonable to study the motion of the centre of mass in the vertical direction in order to learn about the apparent elastic bounce of the body. If the vertical motion of the centre of mass is to be compared to a simple oscillation of an elastic system, then the vertical velocity would be expected to change from zero to a maximum in a time corresponding to one-quarter of the period of the oscillation. In this study, therefore, the step period was divided into four intervals delimited by the instants of zero and maximal vertical velocity of the centre of mass, irrespective of whether or not the body was in contact with the ground. Two of these intervals correspond to the downward deceleration and upward acceleration of the centre of mass, and take place during the ground contact time; the sum of these two intervals is called the effective contact time in this study. The other two intervals correspond to the upward deceleration and the downward acceleration of the centre of mass, and take place during both ground contact and aerial phase; the sum of these two intervals is called effective aerial time in this study.

This procedure has been applied to experimental data obtained in running, trotting and hopping in order to assess if and to what extent the elastic model assumed to govern these systems of locomotion, is tenable. Some of the results have been reported briefly (Cavagna, Franzetti, Willems & Heglund, 1987).

METHODS

The vertical velocity of the centre of mass was determined by analog integration of the signal from a force platform (4 m long and 0.5 m wide) sensitive to the vertical component of the force exerted by the feet on its surface during locomotion. The characteristics of the platform, the principle of the method and the procedure followed to process the platform's signals are described in detail by Cavagna (1975) and, more recently, by Cavagna, Franzetti & Fuchimoto (1983).

For human running we analysed 193 runs over the platform by ten untrained male subjects, weight 75.7 ± 4.99 kg, height 1.77 ± 0.029 m (mean \pm s.d., $n = 10$). The subjects ran across the force platform at a variety of different constant speeds; particular care was taken to explore the range of very low speeds. All of the subjects wore gym shoes.

For animal locomotion 184 records of vertical velocity, previously obtained by Cavagna, Heglund & Taylor (1977), were reanalysed. These records included trotting in a monkey (*Macaca speciosa*, weighing 3.6 kg), two dogs (*Canis familiaris*, weighing 5 and 17.5 kg) and two rams (*Ovis musimon*, weighing 60 and 85 kg); running in a large bird (*Rhea americana*, 22.5 kg) and two smaller birds (wild turkey, *Meleagris gallopavo*, about 7 kg); and hopping in two kangaroos (*Megaleia rufa*, about 20 kg each) and a springhare (*Pedetes cafer*, 2.5 kg).

The vertical velocity tracing was digitized using a sampling interval of 0.5–20 ms depending upon the speed of locomotion. A section of each digitized record was selected that included a total of one to four contiguous steps. Care was taken to select constant speeds of locomotion and to avoid drift in the vertical velocity during the chosen interval (the drift of the horizontal and vertical velocity curves was always smaller than 25% of the sum of the increments in the curves). The selected section of the velocity tracing was then integrated to get the vertical displacement of the centre of mass, S_v , and differentiated to get the vertical acceleration of the centre of mass, a_v (Fig. 1A). The mass-specific vertical stiffness was calculated as da_v/dS_v (Fig. 1B).

The integration of the vertical velocity was made by assuming that the total upward displacement during the integral number of steps chosen was equal to the total downward displacement (solid symbols in the vertical displacement tracings of Figs 2, 3 and 4).

The differentiation of the vertical velocity was made over finite time intervals of 20–40 ms; these intervals proved to be large enough to minimize the noise due to the vibration of the platform (which often made the original force records of the platform impossible to use), and yet small enough to yield a sufficiently sharp tracing of the vertical acceleration. In order to get a 20–40 ms time interval to perform the differentiation including the first and last 10–20 ms of the selected section of the velocity record, the last 10–20 ms of the tracing were attached to the beginning of the section and the first 10–20 ms of the tracing to the end. This procedure often leads to an asymmetry in the velocity tracing with the consequence that the acceleration, as calculated, is not zero at the beginning and end of the tracing (see the a_v tracing shown to illustrate running in Fig. 1A).

The effective contact time, $t_{c,e}$, was measured from the instant of maximum downward velocity to the instant of maximum upward velocity; it was always less than the actual ground contact time, t_c (Fig. 1). The effective aerial time, $t_{a,e}$, was measured from the instant of maximum upward velocity to the instant of maximum downward velocity; it was always larger than the actual aerial time, t_a (Fig. 1).

The aerial time was taken as the time interval during which the sum of the gravitational potential energy plus the kinetic energy of vertical motion remains constant (for example, see Fig. 5 of Cavagna *et al.* 1976: in the present study these energies were measured for this purpose only). The ground contact time was measured as $t_c = T - t_a$, where T is the step period. The ground contact time and the aerial time are indicated by the continuous and the dotted lines, respectively, in Figs 2, 3 and 4. These lines were fitted through the experimental data (not shown) either by eye or by using the least-squares fit method.

The fractions of the vertical displacement ($S_{c,e}$, $S_{a,e}$, S_c and S_a in Figs 2, 3 and 4) are the average of the upward and the downward displacements measured during the indicated fraction of the step period. The upward and downward displacements during these fractions of the step period are, in fact, not necessarily equal. For example, during the ground contact time, the downward displacement of the centre of gravity is always less than the upward displacement due to a landing-take-off asymmetry within the step.

The step length (L) and the forward displacement of the centre of mass taking place during $t_{c,e}$ and $t_{a,e}$ ($L_{c,e}$ and $L_{a,e}$) were calculated by multiplying the duration of the step fraction by the average forward velocity, neglecting the forward velocity changes taking place during the step (Cavagna *et al.* 1976).

For each test, the vertical acceleration was plotted as a function of the vertical displacement (Fig. 1B), and the slope of a line through the data obtained during the effective contact time (corresponding to the positive values of a_v in Fig. 1) was calculated by the least-squares fit method. This slope (having units s^{-2}) is the mass-specific whole-animal vertical stiffness, k/m , where k is the

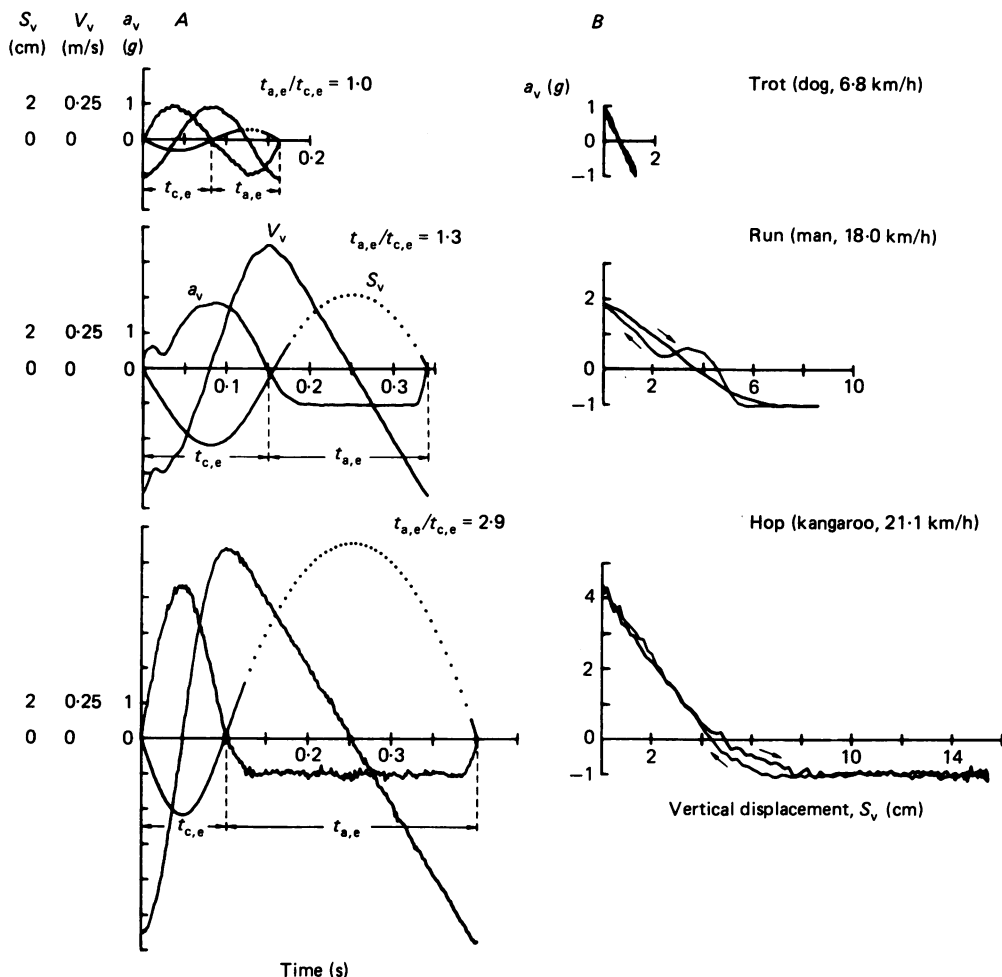


Fig. 1. *A*, the vertical displacement (S_v), velocity (V_v) and acceleration (a_v) of the centre of gravity of the body are plotted as a function of time during a step of trotting at 6.8 km/h for a 5 kg dog (top tracings), running at 18 km/h for a 72 kg man (middle tracings) and hopping at 21.1 km/h for a 21 kg kangaroo (bottom tracings). The vertical acceleration is zero when the vertical force on the ground equals the body weight, 1 g (9.81 m/s²) when the vertical force is two times the body weight and $-1 g$ when the vertical force is nil. The dotted section of the vertical displacement tracing indicates the aerial phase; the time interval between dots is 8 ms for the dog and the man, and 6 ms for the kangaroo; the time interval between points in the continuous section of the tracings is 1 ms for the dog, 2 ms for the man and 1.5 ms for the kangaroo. The symbols $t_{c,e}$ and $t_{a,e}$ indicate the fractions of the step period during which the vertical force on the ground is greater or less, respectively, than the body weight. In trotting the rebound is symmetric because $t_{c,e} = t_{a,e}$ whereas in running at 18 km/h and particularly in hopping the rebound is asymmetric because $t_{a,e} > t_{c,e}$. *B*, the vertical acceleration of the centre of gravity is plotted as a function of the vertical displacement of the centre of gravity for the same steps illustrated in *A*. Positive values of the vertical acceleration refer to $t_{c,e}$, negative values to $t_{a,e}$. The average slope during $t_{c,e}$ was calculated by fitting a straight line through the points by the least-squares method; this slope represents the mass-specific vertical stiffness and amounts to 1433 s⁻² ($r = 0.97$, $n = 83$) for the dog, 416 s⁻² ($r = 0.95$, $n = 76$) for the man and 890 s⁻² ($r = 0.99$, $n = 69$) for the kangaroo.

actual vertical stiffness (N/m) and m is the body mass (kg). The apparent natural frequency of the system over which the body bounces (f_a) was calculated as $f_a = (k/m)^{1/2}/(2\pi)$. For comparison, the frequency of the system was also measured according to the approximation made in the past, that the contact time (t_c) equals one-half the period of resonant vibration, $f_c = 1/(2t_c)$.

RESULTS

The step period (T) and the vertical displacement of the centre of gravity (S_v) are given as a function of speed (\bar{V}_t) by the solid symbols in the two upper tracings of Figs 2 (running), 3 (trotting) and 4 (hopping). In the two lower tracings of the same Figures the filled symbols indicate the step frequency ($f = 1/T$) and the step length ($L = T\bar{V}_t$).

In order to investigate the mechanisms determining the step frequency at different speeds, it is necessary to analyse the events taking place within the step. Since the proposed mechanism is the rebound of the body off the ground, the step period and the vertical oscillation of the centre of mass during the step have been divided, as described above, into two parts: one part taking place when the vertical force is greater than body weight ($t_{c,e}$ and $S_{c,e}$, \square), and another part taking place when the vertical force is smaller than body weight ($t_{a,e}$ and $S_{a,e}$, \triangle). For comparison, the step period and the vertical displacement have also been divided, according to tradition, into parts occurring during the ground contact phase (continuous line) and the aerial phase (dotted lines).

Trotting and slow running: a symmetric rebound

At low speeds of running and most speeds of trotting the vertical oscillation of the centre of gravity during the step is symmetric, i.e. $t_{c,e} \sim t_{a,e}$ and $S_{c,e} \sim S_{a,e}$ (Figs 2 and 3). This holds both in the absence of an aerial phase (at very low speeds) and in the presence of an aerial phase (at greater speeds).

Contrary to the total contact time (t_c), the effective contact time ($t_{c,e}$) may always be compared to a half-period of oscillation of an elastic system. On the other hand, the effective aerial time ($t_{a,e}$) may be compared with the second half-period, strictly speaking, only when the actual aerial phase is nil and the vertical force approaches during the oscillation a maximum of two times the body weight and a minimum of zero. During the aerial phase, the elastic model is not tenable because the restoring force is constant (equal to body weight) and does not depend on the deformation of the system. In spite of this, during trotting and slow running, the duration and amplitude of the lower half of the vertical oscillation of the centre of mass ($t_{c,e}$ and $S_{c,e}$) equal those of the upper half ($t_{a,e}$ and $S_{a,e}$), even in the presence of an aerial phase.

During locomotion on the level the vertical momentum lost and gained during $t_{c,e}$ must equal the vertical momentum lost and gained during $t_{a,e}$. Therefore, in slow running and trotting, the average vertical acceleration of the centre of mass of the body during $t_{c,e}$ and $t_{a,e}$ must be the same in spite of the presence of an aerial phase. In addition, since during $t_{a,e}$ the vertical acceleration cannot exceed $1g$, this also means that during $t_{c,e}$ the average vertical acceleration must be less than $1g$. In fact, in trotting the average acceleration during $t_{c,e}$ attains a maximum of about $0.9g$ in

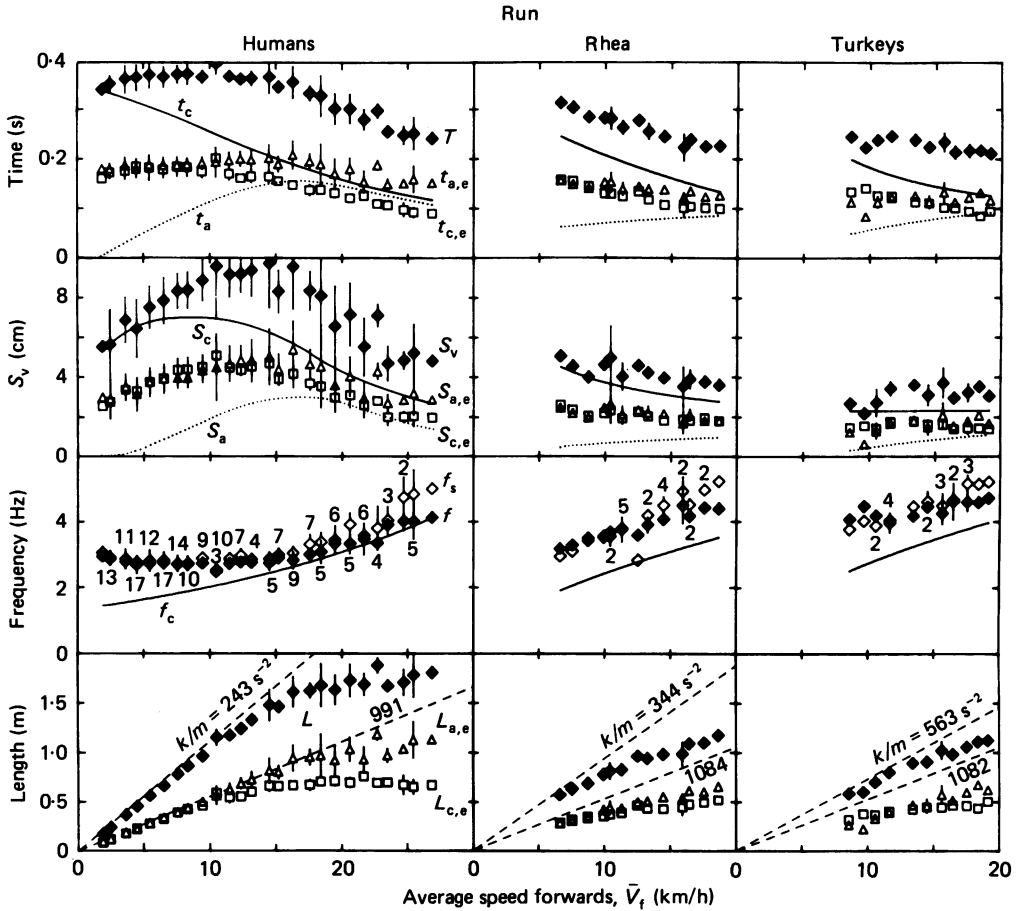


Fig. 2. \blacklozenge indicate, from top to bottom, the step period (T), the vertical displacement of the centre of gravity during the step (S_v), the step frequency ($f = 1/T$) and the step length ($L = T \bar{V}_f$) as a function of the running speed (\bar{V}_f). \triangle indicate the duration of the effective aerial phase ($t_{a,e}$), and the displacement of the centre of gravity during this phase in the vertical direction ($S_{a,e}$) and in the forward direction ($L_{a,e}$). Similarly \square indicate the duration of the effective contact phase ($t_{c,e}$), and the corresponding displacements in the vertical direction ($S_{c,e}$) and in the forward direction ($L_{c,e}$). The continuous lines in the two upper tracings indicate the actual ground contact time (t_c) and the vertical displacement of the centre of gravity taking place during it (S_c); the dotted lines in the same tracings indicate the actual aerial time (t_a) with the corresponding vertical displacement (S_a). In the tracing below, \diamond indicate the apparent natural frequency of the elastic system, f_s , calculated from the stiffness measured as described in the legend of Fig. 1; the continuous line indicates the frequency, f_c , calculated assuming that the actual time of contact corresponds to one half-period of the oscillation of the elastic system. The interrupted lines in the bottom tracing indicate the wavelength, i.e. the forward distance covered during a vertical oscillation of an elastic system having the indicated mass-specific stiffness. The vertical bars indicate the standard deviation of the mean and are drawn when they exceed the size of the symbol; the figures near the symbols indicate the number of items in the mean (when this number is greater than one).

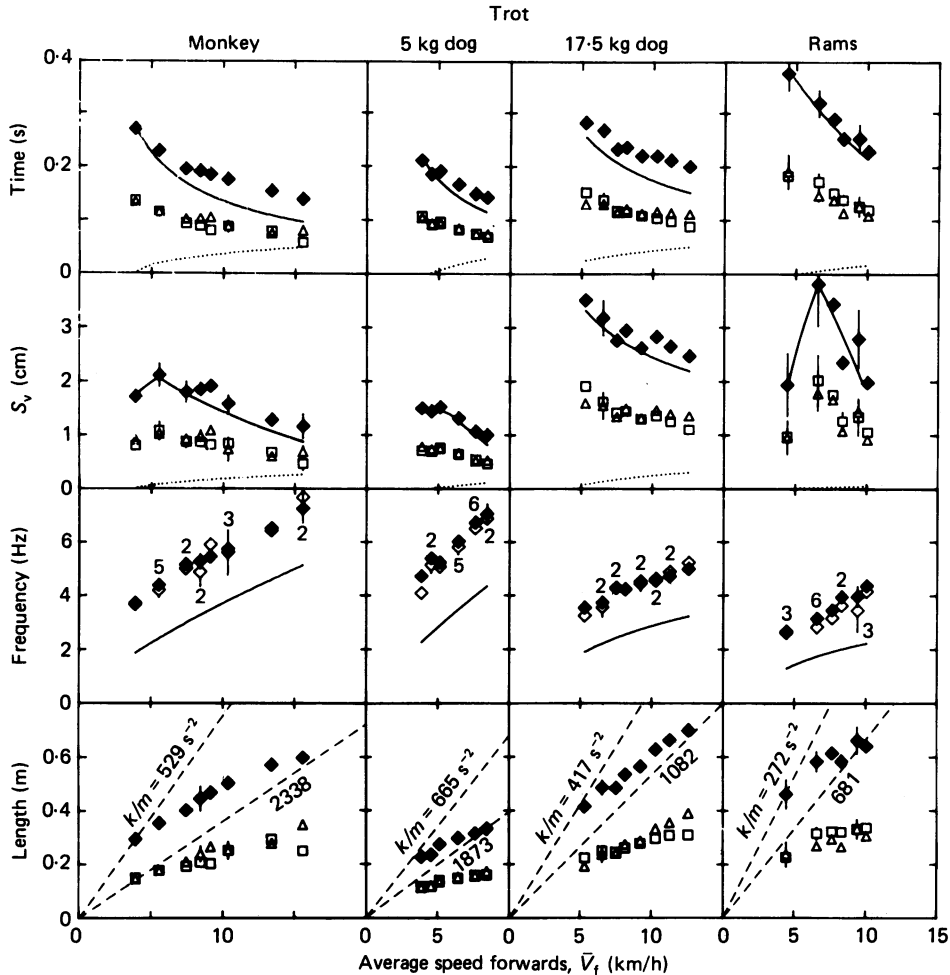


Fig. 3. Data for trotting. See legend to Fig. 2 for explanation.

the bigger dog, 0.6 g in the rams, 0.7 g in the smaller dog and crosses 1 g only at the highest speeds in the monkey. In running the rebound is symmetric until around 11 km/h in humans and 14–15 km/h in birds, when the average acceleration during $t_{c,e}$ becomes greater than 1 g .

It is interesting to note that a division of the step based on the actual ground contact and aerial times (continuous and dotted lines in Figs 2 and 3) shows the largest and most variable asymmetry just when $t_{c,e}$ and $t_{a,e}$ show that the rebound is symmetric.

The stiffness, k/m , increases with the speed of locomotion \bar{V}_f in all of the animals. In humans the stiffness remains about constant up to about 11 km/h and then it also increases with speed. As described in the Methods the stiffness was used to compute the apparent natural frequency of oscillation of the body during the rebound. It can be seen that at low speeds of running and in trotting, the apparent natural frequency of oscillation of the body (f_s , \diamond in Figs 2 and 3), is practically equal to the freely

chosen step frequency (f , \blacklozenge). On the contrary, the frequency calculated on the assumption that the time of contact equals one-half the period of an oscillation (f_c , continuous line), is much lower than f .

The wavelength, which corresponds to the forward distance travelled by a spring-mass system during one complete oscillation with no aerial phase, can be calculated from the equation:

$$\text{wavelength} = \bar{V}_t 2\pi(m/k)^{\frac{1}{2}}. \quad (1)$$

The minimum and maximum values of the mass-specific stiffness, k/m , were used to calculate the maximum and minimum wavelengths as a function of speed; the iso-stiffness lines for each animal are given in the bottom graphs of Figs 2, 3 and 4 (interrupted lines). It can be seen that in trotting and slow running, the wavelength of the oscillation extends over the whole of the step length (i.e. \blacklozenge are bound by the minimum and maximum wavelength lines). This is in contrast to the high speeds of running and to hopping.

In an elastic system the period of the oscillation is independent of its amplitude. This is consistent with some of the present findings. At low speeds of human running the stiffness and the step period are, on average, kept constant while the amplitude of the oscillation increases (in some subjects this amplitude remains constant or even decreases slightly), while in the trot of the monkey and the rams a decrease in the period is accompanied first by an increase and then by a decrease in the amplitude of the oscillation.

In conclusion, the described findings indicate that in trotting and slow running the proposed division of the step period successfully describes locomotion as a continuous succession of vertical oscillations similar to those of an elastic system having a roughly linear force-length diagram during $t_{c,e}$ (Fig. 1*B*). This conclusion cannot be reached with an analysis of the step based on its division into contact and aerial times.

Hopping and fast running: an asymmetric rebound

In hopping and high-speed running the vertical oscillation of the centre of gravity during the step is asymmetric: i.e.

$$t_{c,e} < t_{a,e} \quad \text{and} \quad S_{c,e} < S_{a,e}.$$

This asymmetry usually arises from the fact that the average vertical acceleration during $t_{c,e}$ becomes greater than $1\ g$ whereas during $t_{a,e}$ it cannot exceed $1\ g$. As a consequence, a longer aerial phase is required to dissipate and restore the momentum gained during $t_{c,e}$. The average acceleration during $t_{c,e}$, attained at the highest speeds, is about $1.7\ g$ in humans, $1.2\ g$ in the birds, $3\ g$ in kangaroos and $4\ g$ in the springhare.

At high speeds of trotting in the larger dog the rebound is slightly asymmetric in spite of the fact that the acceleration during $t_{c,e}$ is always less than $1\ g$, suggesting that the described asymmetry is not always bound to the condition described above.

The apparent natural frequency of the bouncing system, f_s , is greater than the step frequency, f , in fast running and hopping, where the rebound is asymmetric. On the

contrary, at high speeds of human running: $f_c \sim f$. In addition, $t_c \sim t_a$ just when $t_{c,e}$ and $t_{a,e}$ diverge. This also shows that at high speeds of human running the old analysis leads to erroneous conclusions. However, during hopping the old and the new analyses give results which are qualitatively similar.

The iso-stiffness lines in Figs 2 and 4 show that in hopping and fast running the

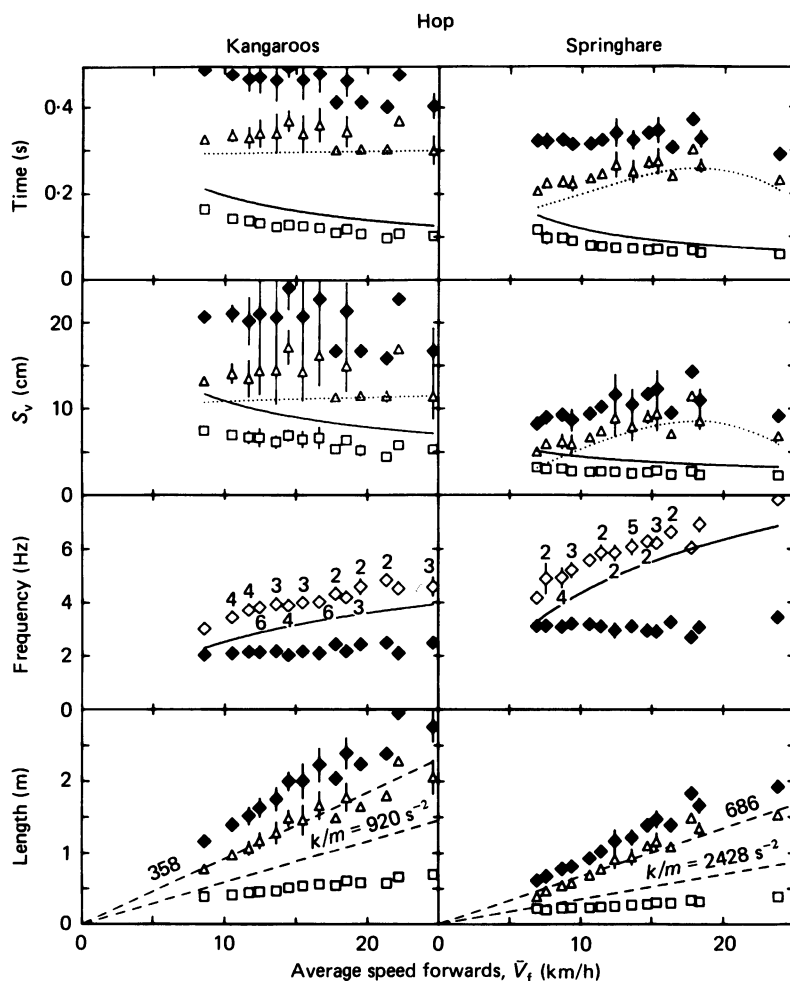


Fig. 4. Data for hopping. See legend to Fig. 2 for explanation.

wavelength of the oscillation extends over a fraction of the entire step length. In hopping the wavelength is, on average, about one-half of the actual step length.

In conclusion, during hopping and high-speed running, locomotion can still be viewed as a succession of bounces of an elastic body having a half-period about equal to $t_{c,e}$. However, in contrast to trotting and low-speed running, the oscillations of the elastic system do not follow one another continuously, but are separated by an aerial phase lasting more than half the period of the vibration.

When does the rebound become asymmetric in running?

In human running the effective step length, $L_{c,e} = t_{c,e} \bar{V}_t$, increases in proportion to the speed, reaching about 0.6 m at a critical speed of 11 km/h (\square in Fig. 2). In this range of speeds $f = f_s = \text{constant}$, the vertical displacement of the centre of gravity increases and, with it, the average vertical force during $t_{c,e}$ (up to two times the body weight). In other words, the increase of the running speed is accompanied by a progressive increase of the deformation of a constant-period system.

Beyond the critical speed, the effective step length, $L_{c,e}$, remains about constant (possibly for anatomical and/or functional limits) with the consequence that $t_{c,e}$ necessarily decreases with the increasing speed. The decrease in $t_{c,e}$ involves an increase in the stiffness, which is revealed by a decrease of the deformation of the system, $S_{c,e}$, and an increase of the average vertical force during $t_{c,e}$. The increase in the vertical force does not completely compensate for the decrease in $t_{c,e}$, with the consequence that the momentum lost and gained, the corresponding vertical displacement, $S_{a,e}$, and time interval, $t_{a,e}$, all decrease with increasing speed (Fig. 2). In spite of this, $S_{a,e}$ and $t_{a,e}$ become progressively greater than $S_{c,e}$ and $t_{c,e}$, indicating a relative increase of the vertical force which leads to the asymmetry described above. An effect of this asymmetry is to contain the reduction of the total period, $T = t_{c,e} + t_{a,e}$, thus limiting the increase of the step frequency.

The above analysis was made on human running, where the speed could be voluntarily decreased to unusual low values in order to expand the range of running with a symmetric rebound. The data obtained on running birds, however, do not seem to be in disagreement with this analysis.

DISCUSSION

The present study gives further support to the idea, formerly based on energetic considerations only, that running, trotting and hopping can be described as a succession of vertical bounces of the body (Cavagna *et al.* 1964, 1977). The complex system of contracting muscles and tendons of the legs and feet (Ker, Bennett, Bibby, Kester & Alexander, 1987) results in an approximately linear relation between vertical force and displacement during the rebound, i.e. the effective contact time (the mean \pm s.d. (n) of the coefficient of correlation, r , is 0.96 ± 0.04 (193) for humans running, 0.94 ± 0.04 (46) for birds running, 0.96 ± 0.04 (63) for trotting and 0.98 ± 0.02 (75) for hopping). The slope of this relationship represents the stiffness of a hypothetical vertical spring over which the whole body bounces each step. This stiffness allows the calculation of a half-period of oscillation which, as a first approximation, can be considered to be equal to the measured effective contact time: the mean \pm s.d. (n) of $\pi(m/k)^{1/2}/t_{c,e}$ is 1.046 ± 0.078 (193) for humans and 1.051 ± 0.069 (184) for the animals.

The elastic model of running naturally poses the question of the relationship between natural frequency of the elastic system and step frequency. For example, since hopping kangaroos utilize nearly the same step frequency over a wide range of speeds (Dawson & Taylor, 1973), the hypothesis has been put forward that this frequency is the resonant frequency of a tuned spring-mass system (Taylor, 1985).

The present study, however, shows that in hopping a clear dissociation exists between step frequency, which remains about constant, and apparent natural frequency of the system which increases markedly with speed (Fig. 4). In general, it is possible to conclude that the apparent natural frequency of the bouncing system equals the step frequency in some running gaits (trotting and slow running: the symmetric bouncing gaits) whereas it is greater than the step frequency in others (hopping and fast running: the asymmetric bouncing gaits). What determines these two different strategies?

Alexander (1984) analysed the shape of the vertical force-time record during the ground contact time and the duration of this time relative to the total step period in order to assess what combination of these two factors leads to a minimum of the mechanical power output; in this model the mass of the legs is ignored. McMahon, Valiant & Frederick (1987) analysed the rebound of the human body in normal and in deep-flexed running, computed the vertical stiffness and showed that a progressively larger fraction of the period of the oscillation takes place during the ground contact time as the stiffness is reduced during deep-flexed running. This is similar to that observed in the present study as the running speed is reduced to very low values. Both McMahon (1985) and McMahon *et al.* (1987) suggest that the step frequency is determined by a compromise between two opposing consequences of a low effective vertical stiffness: a smoother ride and an increased metabolic power; again the mass of the limbs was not taken into account.

The asymmetric rebound, naturally adopted at high speeds of running and in hopping, cannot be explained on the basis of a smoother ride or a smaller power, neglecting the mass of the limbs. In fact, if the step frequency is voluntarily increased above the freely chosen step frequency at a given speed, the average vertical force and vertical displacement during $t_{c,e}$ decrease (i.e. the smoothness of the ride increases) and the power necessary to move the centre of mass, \dot{W}_{ext} , also decreases (unpublished observations by G. A. Cavagna, P. Franzetti & P. Willems).

It seems likely that the asymmetric rebound is adopted, in spite of the greater \dot{W}_{ext} that it involves, in order to limit the increase of the step frequency and therefore the power spent to accelerate the mass of the limbs relatively to the centre of gravity, \dot{W}_{int} . Also in running, as in walking, a compromise is sought that minimizes the total power required, $\dot{W}_{\text{ext}} + \dot{W}_{\text{int}}$ (Cavagna & Franzetti, 1982, 1986; Kaneko, Matsumoto, Ito & Fuchimoto, 1987).

In trotting and running the hind leg can be reset (accelerated forward) during the period of the ground contact phase of the opposite leg and the aerial phase, whereas in hopping both limbs must be reset simultaneously during the aerial phase only. This may explain why the asymmetry of the rebound is larger in hopping than in running and trotting. In conclusion, the step frequency in running, trotting and hopping cannot be predicted by a simple spring-mass system neglecting the mass of the limbs. Motion of the body segments relative to the centre of mass, as well as motion of the centre of mass relative to the surrounding, must be taken into account.

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